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Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae)

by

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..... To Rachel, with love.

Table of Contents

Table of Contents	I
Acknowledgements	III
Thesis Summary	IV
General Introduction	1-15
Rationale for investigating the mechanisms of evolution of the Scarabaeini (Coleoptera: Scarabaeinae)	
Systematics	1
Evolution	2
Feeding Specialisation	3
Phylogenetics	6
Molecules and Morphology	7
Thesis format	8
References	10
Chapter 1	16-85
Revision of <i>Sceliages</i> Westwood, a millipede-eating genus of southern African Dung beetles (Coleoptera: Scarabaeidae)	
Abstract	16
Introduction	17
Materials and methods	19
Genus <i>Sceliages</i> Westwood	24
Key to the species of the genus <i>Sceliages</i> Westwood	28
<i>Sceliages adamastor</i> (Le Peletier de Saint Fargeau and Serville)	30
<i>Sceliages augias</i> Gillet	34
<i>Sceliages brittoni</i> Zur Strassen	37
<i>Sceliages difficilis</i> Zur Strassen	43
<i>Sceliages gagates</i> Shipp	47
<i>Sceliages granulatus</i> sp. nov.	52
<i>Sceliages hippias</i> Westwood	55
Description of mature larvae of <i>Sceliages hippias</i>	60
Biology and Nidification	66
Phylogenetic analysis of the genus <i>Sceliages</i> Westwood	70
Conclusions	77
Acknowledgments	78
References	79
Appendix 1	83



Chapter 2	85-156
Evolution of the Scarabaeini (Scarabaeidae: Scarabaeinae)	
Abstract	85
Introduction	86
Materials and methods	89
Results and discussion	93
Scarabaeini Systematics	104
Flightlessness in the Scarabaeini	111
Food relocation in the Scarabaeini	114
Feeding specialisation in the Scarabaeini	116
Conclusions	117
Acknowledgments	118
References	118
Appendix 1	126
Appendix 2	127
Appendix 3	151
Appendix 4	155
Chapter 3	160-202
Phylogenetic patterns in multiple data sets used for inferring relationships among genera of ball-rolling Scarabaeini (Coleoptera: Scarabaeidae)	
Abstract	160
Introduction	161
Methods and materials	164
Results and discussion	171
Conclusions	189
Acknowledgments	190
References	190
Appendix 1a	197
Appendix 1b	204
General Conclusions	206-207

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Summary

Phylogeny of the Scarabaeini (Coleoptera: Scarabaeidae)

The Scarabaeini comprises some 146 species of ball-rolling dung beetles belonging to the genera *Pachylomerus* and *Scarabaeus*, and *Scarabaeus* subgenera, *Kheper*, *Pachysoma*, *Scarabaeolus*, *Scarabaeus* and *Sceliages*. Their distribution extends throughout the Afrotropical region (including Madagascar) and southern latitudes of the Palaearctic. In this study, 244 morphological characters, including 154 multistate, and 3 biological characters were identified using 28 morphologically diverse members of the tribe. These taxa were polarized against 4 members from related tribes. Molecular sequence data from mitochondrial Cytochrome Oxidase subunit I (1197 bp) and 16S ribosomal RNA (461bp) genes of 25 of these taxa were also obtained in an attempt to further resolve broad phylogenetic relationships inferred from morphology-based hypotheses of tribal evolution.

All data sets were subjected to a battery of weighted and unweighted simultaneous analyses to help recover the most accurate representations of phylogeny. Results show poorly resolved trees with many of the intermediate and basal nodes forming the backbone of each topology collapsed following bootstrap analysis. In concordance with many insect studies involving mitochondrial DNA, many sites exhibited strong A+T nucleotide bias and high interlineage divergences evolving heterogeneously in both genes with transition: transversion ratios reaching saturation. Homoplasious morphological characters appeared to carry more weight than the molecular data leading to an over proportional impact on the latter in combined analyses. Despite a lack topological congruence, phylogenetic signal was present, however, in a number of well-supported relationships that were congruent between the molecular and morphological data.

Molecular evidence indicates the Scarabaeini have origins dating back to at least the mid-upper Miocene (8-18 Million years ago). During this time its members underwent a rapid phase of radiation followed by long periods of divergence. Flightlessness evolved in several lineages along with the polyphyletic evolution of behavioural adaptations associated with food specialization and relocation including pushing, dragging and carrying, or combinations of these techniques. Members of the *Scarabaeus* subgenus *Sceliages* Westwood have evolved extreme necrophagous behaviour of feeding and breeding exclusively on millipedes. Whilst necrophagy is an opportunist strategy utilised by many scarabaeines, only *S. (Sceliages)* beetles have become obligate specialists. Adaptations reported in this study include a positive chemotaxic response to the quinone-based allomones secreted by distressed or injured millipedes. These beetles do not construct food balls and roll them backwards in typical Scarabaeini fashion. Rather, whole or portions of millipedes are pushed away from potential competitors, buried and subsequently dismembered to access the internal tissues for food and reproduction. Phylogenetically, all analyses strongly supported the monophyly of *Sceliages* taxa within *Scarabaeus* S. L. , thereby providing justification of the proposed subgeneric classification of its members. Congruent trends recovered from simultaneous analyses of the morphological and molecular data thus provided a means to review the systematics of the tribe.

Rationale for investigating the mechanisms of evolution of the
Scarabaeini (Scarabaeidae: Scarabaeinae)

The Scarabaeini comprise a behaviourally advanced guild of ball-rollers including *Scarabaeus sacer* L., the first described beetle (Linnaeus, 1758: 345). The rolling of prefabricated spherical balls of food by these beetles was idolised in ancient Egyptian society via the solar deity Khepera, half human and half sacred scarab, who controlled the sun's daily azimuth across the sky (Fig.1).



Fig. 1. Depiction of the ancient Egyptian solar deity, Khepera.

Systematics

The tribe includes approximately 146 species belonging to the genera *Drepanopodus* (Péringuey) *Kheper* Janssens, *Pachylomerus* Bertoloni, *Scarabaeus* L. and *Sceliages* Westwood, and the *Scarabaeus* subgenera *Pachysoma* M'Leay, *Scarabaeolus* Balthasar and *Scarabaeus sensu stricto* (*s. str.*). Their distribution spans the Afrotropical region (including Madagascar) and southern latitudes of the Palaearctic from SE Asia to the Iberian Peninsula. Historically, the name Scarabaeini is relatively recent (Péringuey, 1901) however the tribe was more or less

defined by Reiche (1842) when he morphologically differentiated Ateuchides (Scarabaeini) from Coprides (Mostert and Scholtz, 1986). Janssens' (1949) division of the Scarabaeini into the subtribes Eucraniina, Alloscelina, Gymnopleurina, Canthonina, Sisyphina and Scarabaeina, formed the basis for all major subsequent works involving scarabaeine taxonomy (Balthasar, 1963; Halffter and Matthews, 1966; Ferriera, 1972; Matthews, 1972, 1974; Halffter and Edmonds, 1979, 1982; Halffter and Halffter, 1989). The taxonomic definition of the Scarabaeini was attributed largely to the monophyletic evolution of horizontal relocation ("rolling") of food and often complex nesting behaviours (Halffter and Halffter, 1989). Using Balthasar's (1963) classification, Hanski and Cambefort (1991) promoted the subtribes to tribes (excl. Alloscelina) using morphological distinctions rather than the behavioural correlates shared by the guild. Hanski and Cambefort (1991) also bolstered the number of genera in the tribe to 11 by recognising several genera that are synonyms of the genus *Scarabaeus*. A recent study by Philips *et al.* (submitted) provides evidence to suggest the "rolling" behaviour of these tribes did not evolve monophyletically but two or more times from ancestral "tunnelers".

Evolution

The Scarabaeini are likely to have evolved around the same time as other Scarabaeines during the Cenozoic, stemming from ancestral lineages thought to date back into the lower Cretaceous ca. 98-144 mybp (Krell, 2000) or possibly even the lower Jurassic ca. 180-200 mybp (Scholtz & Chown, 1995; Cambefort, 1991a; Crowson, 1981. However, Krell, 2000, reports there are currently no reliable records of fossil Scarabaeoidea existing before the Lower Cretaceous). Diversification of these scarabaeoids was thought to coincide with the radiation of both angiosperms (Eocene: ca.50 Mya) and mammalian herbivores, particularly artiodactyliforms (lower Oligocene: 35 Mya), with a shift from saprophagy and mycetophagy to coprophagy by adults and larvae (Cambefort, 1991b; Scholtz and Chown 1995. In contrast, see; Chin and Gill, 1996). Fossil dung balls similar to those constructed by modern Scarabaeinae were recovered

from lower Oligocene deposits from Chile (Halffter 1959, quoted by Scholtz and Chown, 1995). Clay covered brood balls and nests recovered more recently from the Chadian Pliocene Australopithecine levels (Duringer *et al.*, 2000) suggests brood ball construction and nesting behaviour seen in modern dung beetles was well established at least 3-3.5 Mya.

The evolution of habitat use by ancestral scarabaeoids was largely influenced by climatic changes taking place during the Cenozoic. Records of grass pollen grains first appeared around the Middle Eocene (Van der Hammen, 1983, quoted by Cambefort, 1991b) when grasslands developed and expanded giving rise to open habitats exploited by many of the radiating artiodactyls and cojointly, coprophagous beetles (Cambefort, 1991b). Modern dung beetles, especially the Scarabaeinae are, at present, more abundant in open habitats than in forests (Halffter and Matthews, 1966; Cambefort and Walter, 1991).

Feeding Specialisation

Whilst the majority of the Scarabaeini consequently specialised in the utilisation of specific food types (e.g. ruminant/non-ruminant dung), resources tend to be patchy and ephemeral. Many of its members therefore become opportunists in exploiting many types of resources including carrion. Equal numbers of *Pachylomerus femoralis* Kirby, for example, were caught in traps baited with carrion, fermenting fruit or several types of dung (Endrödy-Younga, 1982; Doube, 1991). Furthermore, the subgenus *Scarabaeus* (*Scarabaeolus* Balthasar) contains species utilising dung and/or carrion. A courting pair of *S. (Scarabaeolus) xavieri* Ferreira have been observed rolling a carcass of their larger cousin, *P. femoralis* (Forgie, pers. observ.). While dung is likely the preferred diet of the majority of the Scarabaeini, some degree of opportunism is displayed in desert dwelling species. *S. (Scarabaeolus) rubripennis* (Boheman) has been observed rolling pieces of millipede along in the same manner it moves balls of dung (Mostert and Scholtz, 1986).

In contrast, few species in the tribe have become truly specialist feeders deviating from the archetypal feeding strategies of the majority of the tribe and adopting “aberrant” feeding behaviours. Moreover, the Scarabaeini contain species that are non-rollers (see Halffter and Halffter, 1989) and others that don’t roll food backwards but push, drag and carry it forwards. Flightless *Scarabaeus* (*Pachysoma* M’Leay) utilise dry dung pellets and/or detritus that are dragged into pre-prepared burrows in sandy soil and buried in moist sand for rehydration in feeding and nesting galleries (Holm and Scholtz, 1979; Scholtz, 1989). Whilst unique in the Scarabaeini, convergence in this feeding behaviour is reported in the geotrupine, *Geotrupes* (*Thorectes*) *sericeus* Jekel (Klemperer and Lumaret, 1985), by most of the 18 species of southern neotropical Eucraniini (Zunino, 1983; Zunino *et al.*, 1989), and by several Western Australian canthonines and onthophagines such as *Coproecus* Reiche, *Mentophilus* Castelnau, *Tesserodon* Hope, *Onthophagus* Latreille (Matthews, 1974).

Some of the most specialised members of this tribe belong to the genus *Sceliages*, which exclusively utilise millipedes (Diplopoda) for food and reproduction. Millipede necrophagy has long been known in the Scarabaeinae (Halffter and Matthews, 1966: 25-34). Facultative opportunistic use of millipede carcasses by *Scarabaeus* (*Neateuchus* (syn.)) *proboscideus* Guérin, *S. satyrus* (Boheman), and *S. (Scarabaeolus) flavicornis* (Boheman), has been observed (Forgie and Scholtz, unpubl.). Necrophagy of millipedes has also been recorded in several species in two other tribes. In the Onthophagini, several species of *Onthophagus* Latreille, including *O. bicavifrons* d’Orbigny, and *O. latigibber* d’Orbigny, were attracted to fresh millipede carcasses (Krell *et al.*, 1997, 1998; Krell, 1999). Neotropical canthonines, *Canthon cyanellus cyanellus* Le Conte, and *C. morsei* Howden, utilize both live injured and dead diplopods (Villalobos *et al.*, 1998), whilst *Deltochilum kolbei* Paulian, (Halffter and Matthews,

1966) and *D. valgum acropyge* Bates, (Cano, 1998) are known to actively prey on live millipedes.

Various quinone-based defensive allomones are secreted particularly in spirobolid and spirostreptid millipedes to repel attack by predators (Krell *et al.*, 1998). Two species of the orders Spirostreptida and Julida were found to use quinonous defensive secretions as pheromones (Haacker, 1974), and is likely to be a secondary function for many species of millipedes using these secretions. Necrophagous onthophagine scarabaeids are reported to be attracted to millipede secretions used as repellents (Krell *et al.*, 1997, 1998; Krell, 1999) and are also likely to be attracted to the quinonous secretions used as pheromones by millipedes during copulation (Kon *et al.*, 1998). Positive chemotaxis to the defensive secretions of millipedes by *Sceliages* has not been tested prior to this study. Live, injured and freshly dead millipedes all attract *Sceliages* suggesting quinone-based secretions play a role in attracting these beetles (Krell, 1999; Forgie *et al.*, 2002).

With the description of the new species there are now seven in the genus *Sceliages*, all restricted to southern Africa. Members of the genus are rarely encountered in the wild and are likely to be mistaken for *Scarabaeus* L. Furthermore, specimens of *Sceliages* are rare in collections and often misidentified or unidentified. The biology of *Sceliages* has, to date, not been studied. Zur Strassen's (1965) revision of the genus was based on relatively few specimens held in several museums in Europe and southern Africa and left many open questions including the locality of several of the species types. Thus, the rationale to case study this genus which is perhaps the least known yet one of the most specialized of the Scarabaeini is realized.

Very few phylogenetic studies have centred exclusively on the Scarabaeini. Mostert and Scholtz (1986) considered the flightless Neotropical Eucraniini as the tribe closest to the ancestral stock that gave rise to the Scarabaeini. Although species included in the Eucraniini possess more plesiomorphic characters than those in the Scarabaeini, both tribes share a number of synapomorphies. Mostert and Scholtz (1986) also used members of the Gymnopleurini, considered the next closest tribe to the in-group, to test the relative apomorphies of characters in the Eucraniini that were effected by changes associated with flightlessness. The close association between the Eucraniini and the Scarabaeini was believed to be based on convergence of distinct apomorphic characters (Zunino *et al.*, 1989). We test the hypothesis that the close relationship between the Eucraniini and the Scarabaeini is the result of morphological convergence and is not due to common ancestry.

Barbero *et al.* (1998) examined interspecific relationships between 32 species of *Scarabaeus* distributed throughout the whole geographic range of the genus. Three distinct clades corresponding to subgenera *Scarabaeus*, *Scarabaeolus* and *Ateuchetus* Bedel, were identified. The later, with the exception of *S. catenatus* (Gerstaecker) and *S. savignyi* M'Leay, being restricted to the western Palaearctic. Most recently, Harrison and Philips (2003) investigated the evolution of flightless *Scarabaeus* (*Pachysoma*) restricted to western coastal regions of Southern Africa. Their phylogenetic analysis showed a clear basal dichotomy in the tribe's evolution between members of the scarabaeini that retained flight and those who lost it. Members of the subgenus *Pachysoma* were depicted as the most evolved of the flightless clade sharing with other flightless lineages a complex of convergent morphological characters associated with existence in arid desert environments.

To date, only morphological character sets have been used in phylogenetic studies to infer inter- and/or intra-generic relationships among members of the Scarabaeini (Mostert and Scholtz, 1986; Barbero *et al.*, 1998; Harrison and Philips, 2003). These studies were based on relatively small amounts of data that may have generated inaccurate or biased phylogenetic reconstructions (see Hillis, 1998; Grandcolas *et al.*, 2001). A recent study of Scarabaeinae (Philips *et al.*, 2004) was based on large morphological data sets comprising more than 200 characters in an attempt to improve phylogenetic signal and generate more robust hypotheses. Both studies support congruence in the polyphyletic evolution of ball-rolling and feeding behaviours deviating from coprophagy. However, a high degree of character homoplasy is reported in the scarabaeines, likely the product of nonheritable information brought about by environmental influences (Hillis, 1987).

Molecules and Morphology

The advent of Polymerase Chain Reaction (PCR; Saiki *et al.*, 1988) marked a proliferation in the use of sequenced regions within mitochondrial DNA (see Simon *et al.*, 1994), and more recently, nuclear ribosomal DNA in insect molecular systematics (see Caterino, Cho and Sperling, 2000). Within the former of these classes, the Cytochrome Oxidase subunit I (COI) and COII markers have historically proven useful in providing sufficient phylogenetic signal in estimating relationships corresponding to interspecific levels of recent divergence within Coleoptera (e.g. Emerson and Wallis, 1995; Langor and Sperling, 1997; Kobayashi *et al.*, 1998; Cognato and Sperling, 2000) including within the Scarabaeinae (Villalba *et al.*, 2002). In contrast, the highly conserved 3' region of the large ribosomal subunit (16S) of mitochondrial DNA has proven more effective at addressing deep levels of divergence evident among distantly related taxa (DeSalle, 1992; Derr *et al.*, 1992). Similarly, 18S nuclear ribosomal RNA has also been useful for resolving basal relationships in higher level phylogenetic studies (Chalwatzis *et al.*, 1996; Caterino *et al.*,

2002). Given that different genes evolve at different rates and the same gene may have different rates of evolution in different lineages (Lunt *et al.*, 1996), the quest to obtain suitable levels of variability has become increasingly important in attempting to resolve close, intermediate and deep levels of divergence where possible in any phylogenetic study.

Thus, the value of a total evidence approach to utilising multiple data sets and analysing them separately (Bull *et al.*, 1993; Miyamoto and Fitch, 1995), or combined (Kluge, 1998) and analysed simultaneously (Nixon and Carpenter, 1996; Baker and DeSalle, 1997) has become apparent. Indeed, multiple data sets are integral in many phylogenetic studies using molecular markers (Vogler and DeSalle, 1993; Funk *et al.*, 1995; Vogler and Welsh, 1997; Funk, 1999; Mardulyn and Whitfield, 1999; Durando, *et al.*, 2000) and morphology (Lafay *et al.*, 1995; Whiting *et al.*, 1997; Silvain and Delobel, 1998; Joy and Conn, 2001; Wiebelen, 2001; Wiegmann *et al.*, 2002).

Thesis Format

Each of the three chapters are compiled as individual papers for publication. Each chapter contains its own reference list and appendices. Both the general introduction and conclusion are tailored from the introduction and conclusions of the respective chapters to pull together the autonomy of chapters written as papers. The first chapter is published in *Invertebrate Systematics* (formerly *Invertebrate Taxonomy*) appearing in the December 2002 issue (Vol. 16(6)). It comprises a revision and phylogeny of the genus *Sceliages* Westwood. A new species is described from the semi-arid western parts of Southern Africa (habitus illustration appears on the cover of *Invertebrate Systematics*, 16(6)) and neotypes are assigned to 2 species following a detailed search for missing types. Moreover, the authors provide for first time a larval

description of one species and give details of the remarkable biology of members of the genus feeding on Diplopoda.

The second chapter is accepted and in press at *Systematic Entomology* at time of binding. It forms the principal phylogenetic analysis for the tribe based in a suite of 246 adult morphological and behavioural characters. Several hypotheses are rigidly tested and discussed in relation to the evolution of flightlessness, ball-rolling, and feeding specialization. A new classification proposes the maintenance of only 2 genera, *Scarabaeus* and *Pachylomerus* and 3 sub-genera i.e. *Scarabaeus* S. Str., *Scarabaeolus* and *Pachysoma*. Of the remaining genera, *Kheper* and *Sceliages* are demoted to sub-genera and *Drepanopodus* is synonymised with *Scarabaeus*.

The third chapter is submitted to *Molecular Phylogenetics and Evolution* in February, 2004. This chapter introduces a molecular component to the tribal phylogeny by sequencing portions the COI and 16S rRNA mitochondrial genes as likely candidates for simultaneous analyses with and without morphological data to resolve as many of the relationships as possible between the close and not so closely related exemplars of the Scarabaeini. In doing so, the authors associated with this paper hope to compare the molecular evolution and phylogenetic utility of these two genes and assess the level of congruence these analyses hold with the morphology-based hypotheses presented in chapter two, and the relatedness between the Scarabaeini and the morphologically similar eucraniines. The molecular phylogenies are then used to assess the proposed tribal classification presented in the second chapter.

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